PARAPHYLY AND POLYPHYLY IN THE WORLDWIDE TRIBE RUBIEAE (RUBIACEAE): CHALLENGES FOR GENERIC DELIMITATION[1,2]

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ABSTRACT

On the basis of multidisciplinary studies on the tribe Rubieae, we contribute to the current discussion on paraphyly and supraspecific taxa that do not contain all descendant species of an ancestral clade. Rubieae belong to the large, predominantly tropical and woody family Rubiaceae and include possibly ≤ 1000 mostly temperate and herbaceous species with worldwide distribution. Our studies span distinctive groups throughout the tribe, consist of a maximum parsimony analysis of plastid *atpB-rbcL* and *rpL32-trnL* DNA sequences, and are summarized in a condensed strict consensus tree. A corresponding two-dimensional scheme illustrates alternative hypotheses for phylogenetic relationships among all major Rubieae clades identified. The small relictual genus *Kelloggia* Torr. in Benth. & Hook. f., formerly excluded from the Rubieae, is supported as a remnant of the ancestors of the tribe. *Didymaea* Hook. f. and *Rubia* L. represent early phylogenetic side lines. All other Rubieae form a large monophyletic crown group with the traditional genera *Asperula* L. being polyphyletic and *Galium* L. paraphyletic. Changes in the circumscription of these and other genera are thus inevitable. The necessity of accepting paraphyletic taxa as well as the positive and negative aspects of taxonomic splitting versus lumping within Rubieae are discussed. Additionally, lectotypes are designated for one section of *Asperula*—*Asperula* sect. *Dioicae* Airy Shaw & Turrill, typified by *A. conferta* Hook. f.—and for three sections of *Galium*—*Galium* sect. *Leiogalium* (DC.) Ledeb., typified by *G. sylvaticum* L.; *Galium* sect. *Lophogalium* K. Schum., typified by *G. multiflorum* Kellogg; and *Galium* sect. *Depauperata* Pobed., typified by *G. songaricum* Schrenk ex Fisch. & C. A. Mey.

Key words: *Asperula*, classification, evolution, *Galium*, *Kelloggia*, lumping, phylogeny, *Rubia*, Rubiaceae, Rubieae, splitting.

Important taxonomic questions that arise in the current field of biosystematics are (1) What principles should be used to build supraspecific taxa? (2) How should molecular and morphological evidence be balanced and incorporated? and (3) How should paraphyletic taxa that do not include all descendants from their common ancestral clade be dealt with? As a contribution to the current discussion of such key questions in biodiversity research, we present molecular and other evidence for relationships within the worldwide tribe Rubieae, subfamily Rubioideae of the giant family Rubiaceae. As a prerequisite for the correct circumscription, grouping, and naming of the clades recognized, we open with a brief survey of > 250 years of traditional taxonomy of the tribe and list all relevant genera and sections. Comments on key characters, ecogeographical differentiation, and internal structure of the accepted major clades follow. As general conclusions, we demonstrate positive aspects of careful splitting over excessive lumping within Rubieae and the paraphyletic nature of otherwise well-founded supraspecific taxa. In order to achieve such an improved classification, we prepare a subsequent, species-based, and fully documented phylogenetic study of the tribe.

TRADITIONAL CIRCUMSCRIPTION AND TAXONOMIC SUBDIVISION OF THE TRIBE RUBIEAE

The majority of what currently constitutes the tribe Rubieae was already assembled in the pre-Linnean literature as the Stellatae. This group was based mainly on its stipules transformed into leaflike elements arranged in whorls with the true, opposite leaves. Later, pluricolpate pollen grains were recog-

[1] We are grateful to the Austrian Academy of Sciences and the Austrian Science Fund (FWF) for financial support, to the Faculty Center of Biodiversity (former Institute of Botany), University of Vienna, and to Tod Stuessy, former Head of the Department for Systematic and Evolutionary Botany, for lab facilities and generous support. Numerous colleagues throughout the world and various herbaria (B, CAS, GH, W, WU) have helped with valuable material. Furthermore, our thanks go to Jean-François Manen and Alessandro Natali (formerly at the Conservatoire et Jardin Botanique of Geneva) for the DNA sequencing of many specimens (including the genus *Mericarpaea*), to Valerie Soza (University of Washington, Seattle) for stimulating contacts and useful suggestions, and to many other friends for help and advice.

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doi: 10.3417/2012088

nized as important for the circumscription of the tribe.

A brief historical survey of the internal taxonomic structure of Rubieae and an examination of Appendix 1 show that the genera *Asperula* L., *Crucianella* L., *Galium* L., *Rubia* L., *Sherardia* L., and *Valantia* L. were all recognized by Linnaeus in 1753, with *Cruciata* Mill. recognized by Miller in 1754. De Candolle (1830) formalized the Stellatae as a tribe of Rubiaceae, accepted most of the older genera, and partly subdivided them into infrageneric but unranked groups. Subsequently, these groups were formalized as sections within *Asperula* (*Asperula* sect. *Cynanchicae* (DC.) Boiss.) and within *Galium* (*Galium* sect. *Aparine* W. D. J. Koch, *Galium* sect. *Cruciata* W. D. J. Koch, *Galium* sect. *Eugalium* (DC.) W. D. J. Koch (= *Galium* sect. *Galium*), *Galium* sect. *Leiogalium* (DC.) Ledeb., *Galium* sect. *Platygalium* (DC.) W. D. J. Koch, and *Galium* sect. *Vaillantioides* W. D. J. Koch).

Intensified studies on the floras of southeastern Europe and southwestern to central Asia in the first half of the 19th century led to the description of the additional genera *Callipeltis* Steven, *Mericarpaea* Boiss., and *Microphysa* Schrenk, plus new sections of *Asperula*: *Asperula* sect. *Cruciana* Griseb., *Asperula* sect. *Glabella* Griseb., *Asperula* sect. *Hylaea* Griseb. (later transferred to *Galium* as *Galium* sect. *Hylaea* (Griseb.) Ehrend.), and *Asperula* sect. *Phuopsis* Griseb. (later elevated to genus as *Phuopsis* (Griseb.) Benth. & Hook. f.); and of *Galium*: *Galium* sect. *Aparine*, *Galium* sect. *Kolgyda* Dumort., *Galium* sect. *Leiogalium*, *Galium* sect. *Microgalium* Griseb., and *Galium* sect. *Thliphthisa* Griseb. (later transferred to *Asperula* as *Asperula* sect. *Thliphthisa* (Griseb.) Ehrend.). In the second half of the 19th century the newly described genus *Didymaea* Hook. f. (Central America) was included within the Rubieae in spite of its typical Rubiaceae stipules, but with pluricolpate pollen grains. During the same period we register the publication of the genera *Relbunium* (Endl.) Benth. & Hook. f. (mostly in South America, now part of *Galium* sect. *Platygalium* s.l.) and *Leptunis* Stev. (Southwest to Central Asia, now an annual member of *Asperula*), as well as *Galium* sect. *Aparinoides* (Jord.) Gren., *Galium* sect. *Leptogalium* Lange in Willk., and *Galium* sect. *Trachygalium* K. Schum. Major additions of supraspecific Rubieae taxa in the 20th century were *Asperula* sect. *Dioicae* Airy Shaw & Turrill and *Asperula* sect. *Hexaphylla* Ehrend., as well as *Galium* sect. *Cymogalia* Pobed., *Galium* sect. *Depauperata* Pobed., *Galium* sect. *Jubogalium* Ehrend., and *Galium* sect. *Orientigalium* Ehrend., and the generally neglected North American genus *Bataprine* Nieuwl. (now part of *Galium* sect. *Platygalium* s.l.). *Kelloggia* Torr. in Benth. & Hook. f., a genus with two species (in East Asia and North America), has been considered a member of the tribe Paederieae (Robbrecht, 1988; Nie et al., 2005) because it has typical Rubiaceae stipules and tricolpate pollen grains; only Robbrecht and Manen (2006) have recently included it into the Rubieae (see below).

In retrospect and in addition to the references cited in Appendix 1, traditional contributions toward supraspecific taxa within Rubieae were made available on a worldwide basis by de Candolle (1830) and Schumann (1897); for Europe, the Mediterranean, and southwestern Asia by Koch (1843), Grisebach (1844), Boissier (1875), Ehrendorfer (1975), and Ehrendorfer et al. (1976, 1982, 2005); for Russia and Central to East Asia by Ledebour (1844), Shishkin et al. (1958), Jelenevsky et al. (2003), and Chen and Ehrendorfer (2011); and for the Americas by Dempster and Stebbins (1968) and Dempster (1980, 1982, 1990).

DNA Sequences and Phylogenetic Relationships among Taxa of Rubieae

The first analytical DNA studies on members of the tribe Rubieae date back to the 1990s: Ehrendorfer et al. (1994), Manen et al. (1994), Natali and Manen (1995), and Natali et al. (1995, 1996). Particular attention has been given to the *atpB* promoter region by Manen and Natali (1995, 1996) and Manen (2000). Further studies have concentrated on the genus *Kelloggia* (Nie et al., 2005) or have gone beyond the tribe (Bremer & Manen, 2000; Robbrecht & Manen, 2006). Recently, more extended and detailed analyses within the tribe have been conducted by Soza and Olmstead (2010a, 2010b) and Ehrendorfer et al. (2011, and in prep.). Using different plastid markers, these studies support each other and allow for an increasingly improved recognition of all major Rubieae clades. Their circumscription and relationships can be much more clearly demonstrated now (Figs. 1, 2) than was possible before, on traditional morphological, karyological, and ecogeographical evidence alone.

All available DNA-supported phylogenies place the disjunct genus *Kelloggia* (clade I, Figs. 1, 2) with two species (*K. chinensis* Franch., eastern Asia; *K. galioides* Torr., western North America) at the base of the traditional Rubieae, in spite of the presence of a plesiomorphic 50-bp sequence in the *atpB* promotor region, characteristic for subfamily Rubioideae, but deleted in all other Rubieae (Nie et al., 2005). Outgroups of the tribe from all remaining Rubiaceae–

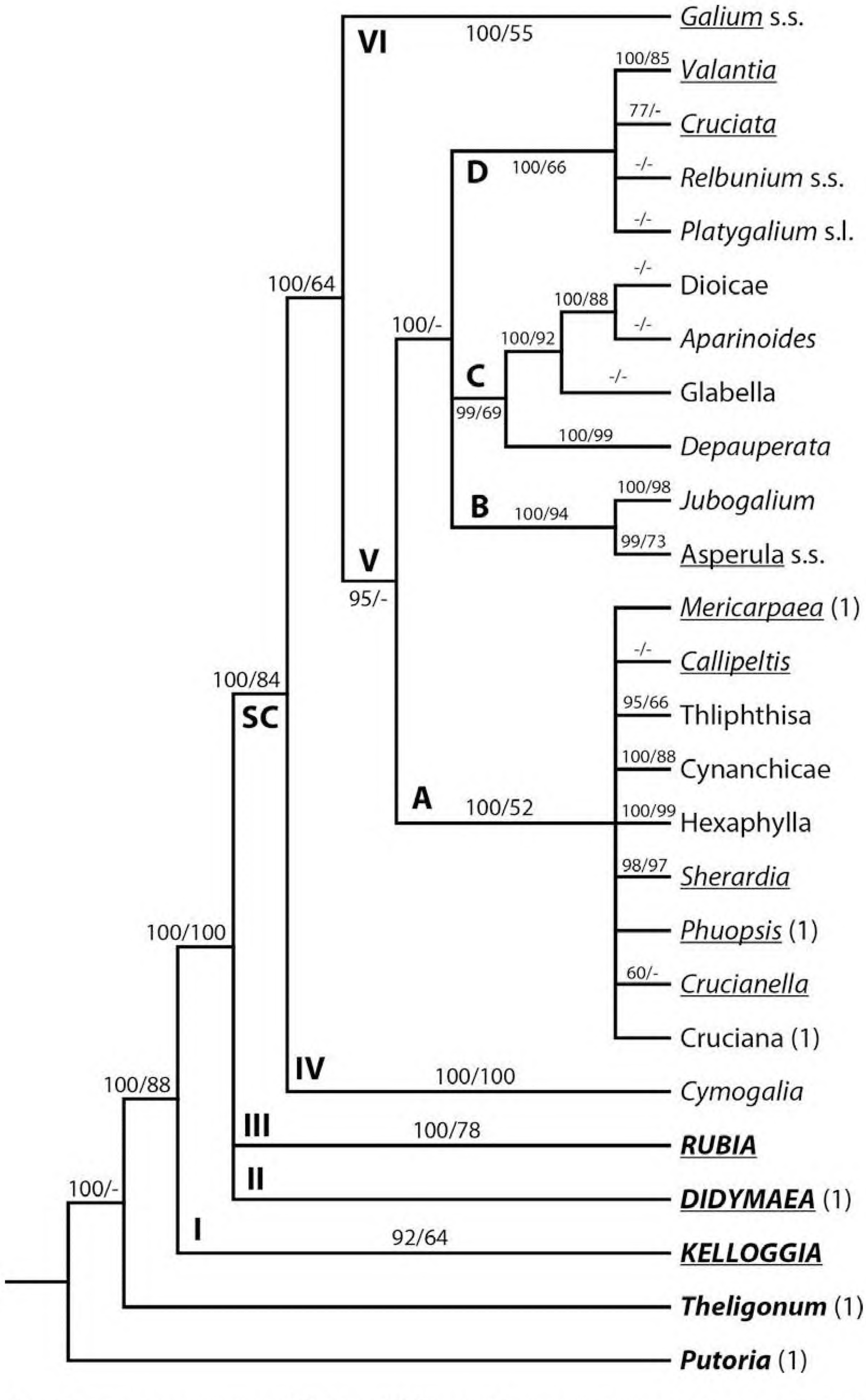


Figure 1. Condensed strict consensus tree of Rubieae (Rubiaceae) from a maximum parsimony analysis of the plastid *atpB-rbcL* and *rpL32-trnL* intergenic sequences of 254 worldwide accessions and 167 species, representing currently accepted 12 genera in Rubieae (underlined) and major sections within *Asperula* L. and *Galium* L., together with two outgroup genera (*Putoria* Pers. and *Theligonum* L.). Numbers on branches refer to posterior probabilities followed by bootstrap values. The main clades of Rubieae are marked with numerals: I (*Kelloggia* Torr. in Benth. & Hook. f. = Kelloggiinae), II + III (*Didymaea* Hook. f. + *Rubia* L. = Rubiinae) and SC (superclade *Galium* s.l.) with IV, VA–D, and VI. Sections published under *Asperula* are in normal script without italics; sections under *Galium* are in italics; accepted genera of Rubieae are in boldface capitals and underlined, outgroup in boldface, lowercase, and not underlined. Clades represented by only one accession are marked "(1)." Publication of the underlying detailed and fully documented plastid DNA phylogeny of all accessions studied is in preparation.

Rubioideae and in increasing phylogenetic distance are the morphologically strongly deviating genera *Theligonum* L. (Theligoneae) and *Putoria* Pers. (= *Plocama* Aiton s.l., Putorieae). Bremer and Eriksson (2009) estimate the divergence of the Rubieae (including *Kelloggia*) from *Theligonum* at ca. 28.6 Ma (million years ago; Late Oligocene), and Nie et al. (2005) at ca. 22.8 Ma (Early Miocene). Within the

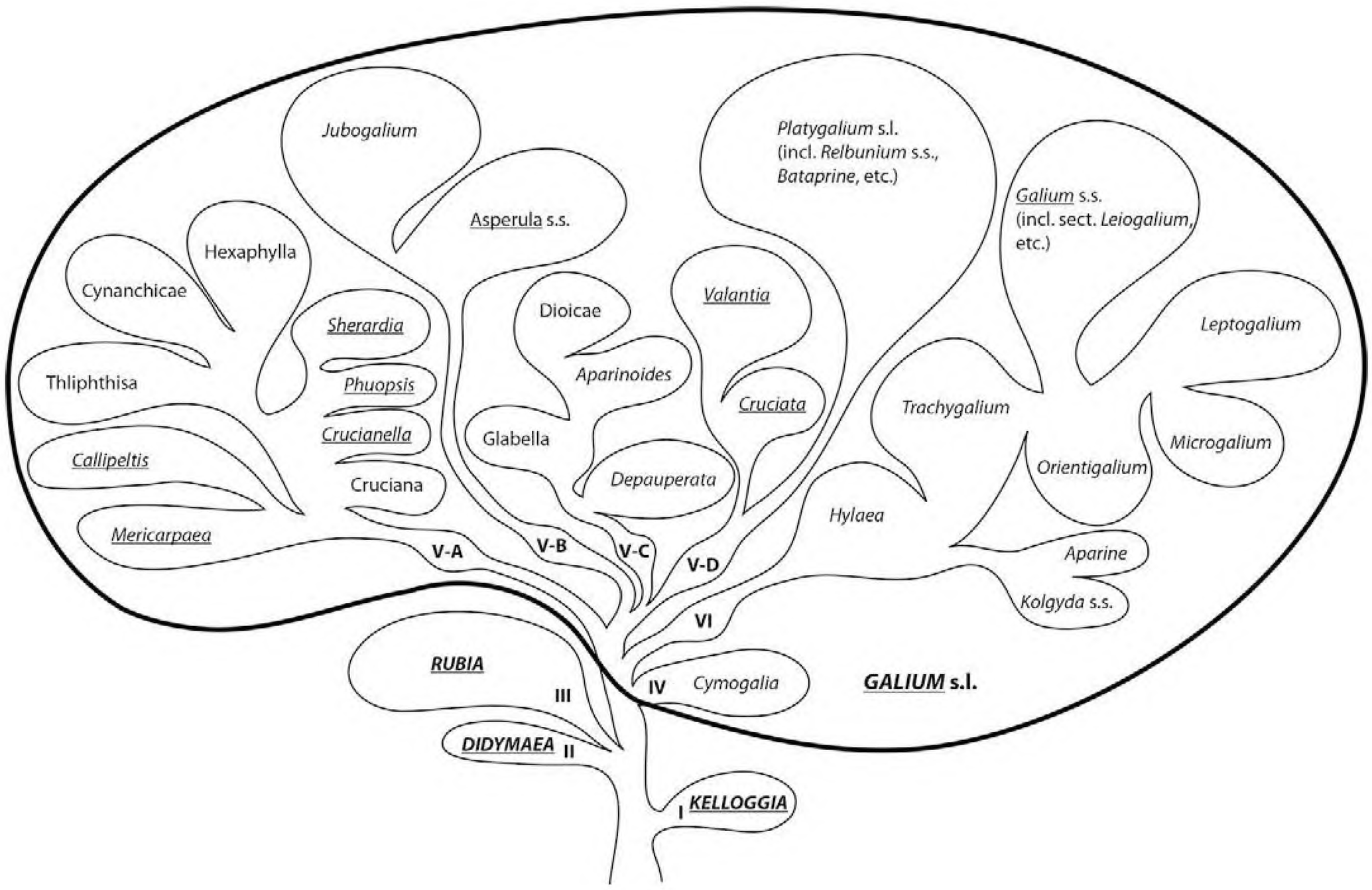


Figure 2. Proposed phylogenetic classification of Rubiaceae–Rubieae with the alternative hypotheses of lumping versus splitting. Lumping: all clades within the thicker encircling line become a single large genus *Galium* L. s.l.; only *Rubia* L., *Didymaea* Hook. f., and *Kelloggia* Torr. in Benth. & Hook. f. remain as segregate genera. Splitting: all separately named clades within IV and VA–D are recognized at a generic level, whereas the single clade VI corresponds to *Galium* s. str. Names currently recognized as genera are underlined. Sections traditionally recognized within *Asperula* L. are in normal script; sections within *Galium* are in italics. The numerals I–VI correspond to clades I–VI in Figure 1, with V including the species groups A–D. The thick, encircling line demarcates the superclade SC (including clades IV–VI) seen in Figure 1.

entire family, *Kelloggia* is the first clade to exhibit the apomorphy of hooked bristles on its dry mericarps, a most efficient character for fruit dispersal. This character becomes widespread within the rest of the tribe. Except for its true, inconspicuous stipules and its tricolpate pollen grains (plesiomorphic characters in the family), *Kelloggia* corresponds perfectly with other Rubieae. It qualifies as close to hypothetical ancestors of the tribe and definitely should be included, possibly as a subtribe Kelloggiinae (as already proposed by Robbrecht & Manen, 2006). A problem emerges if *Kelloggia* is not regarded as sister but rather as a surviving relic of Rubieae ancestors. This would make Keloggiinae paraphyletic from the standpoint of cladistics because the subtribe then should include all of its increasingly apomorphic extant descendants (cf. Schmidt-Lebuhn, 2011: fig. 2, X+C vs. A, B).

Didymaea (clade II in Figs. 1, 2), a small Central American genus of ca. 14 species, and *Rubia* (clade III in Figs. 1, 2), a Eurasian to African genus of ca. 80 species, partly retain typical plesiomorphic stipules. However, most taxa of *Rubia* already exhibit the innovation of conspicuous apomorphic, leaflike stipular elements in whorls with true leaves. Instead of tricolpate pollen, both genera develop pluricolpate pollen grains and share fleshy mericarps, both further apomorphic characters in the tribe. These two disjunct genera form a strongly supported superclade in most phylogenies (e.g., in Soza & Olmstead, 2010a) and apparently have diverged (or budded) early from the main line of the tribe. They can be regarded as subtribe Rubiinae s. str. of Rubieae.

The remaining ca. 900 species of Rubieae form a worldwide superclade (labeled SC in Fig. 1) and should be designated as a third subtribe based on *Galium* s.l. This superclade includes six highly supported clades identified as IV, VA–D, and VI (Figs. 1, 2). With the exception of the newly resolved clade IV, Soza and Olmstead (2010a) recently have also found all these clades independently and to be well supported by other DNA markers. Figures 1 and 2 illustrate this main result of our plastid DNA analyses: there is clear evidence that *Asperula* (appearing independently in clades VA–C) and *Galium* (rooted in clade IV and reappearing in VB–D and VI) are polyphyletic or paraphyletic in their present, traditional, and artificial circumscription.

The most basal branch of the superclade (SC) is clade IV (Figs. 1, 2) with the monotypic *Galium* sect. *Cymogalia*. It consists only of *G. paradoxum* Maxim., whose DNA has not been studied before. This is a sylvicolous perennial with a disjunct occurrence in the Urals (western Russia and northwestern Kazakhstan), whereas its main distribution is in eastern Asia. The inflorescence and hooked mericarp bristles of *Galium* sect. *Cymogalia* are remarkably similar to *Kelloggia*, but it deviates by having whorls of two larger leaves and two smaller leaflike stipules, both with a plesiomorphic camptodromous venation and by the apomorphic rotate (not funnel-shaped) flowers. One could interpret *Galium* sect. *Cymogalia* as a relic of an ancestral paraphyletic group that has given rise to the remaining, more apomorphic Rubieae clades VA–D and VI (see Fig. 2).

Clade VA (Figs. 1, 2), centered in southwestern Asia and the Mediterranean, has been recognized since the report published by Natali et al. (1995) as the *Sherardia* clade and was confirmed as clade IV by Soza and Olmstead (2010a). This group is mainly characterized by an elongate corolla tube with five to four lobes and usually glabrous, dry mericarps. Traditionally, these taxa have been relegated to separate genera, to *Phuopsis*, *Sherardia* (both with one species), and *Crucianella* (ca. 35 species), and to several sections in *Asperula*. This variability ranges from the rather plesiomorphic *Asperula* sect. *Cruciana* (ca. 10 species) with funnel-shaped and 5-merous flowers to the increasingly apomorphic *Asperula* sect. *Cynanchicae* ($\leq$ 80 species), *Asperula* sect. *Hexaphylla* (ca. 12 species), and *Asperula* sect. *Thliphthisa* (ca. 24 species) with 4-merous flowers, the latter even with partly rotate corollas. It is surprising that, according to their plastid DNA data, the extremely aberrant and apomorphic, annual, and autogamous genera *Callipeltis* (three species) and *Mericarpaea* (one species) are only loosely related to each other but clearly belong to clade VA (Figs. 1, 2). Both have inconspicuous rotate flowers, with *Callipeltis* characterized by enlarging inflorescence bracts that favor anemochorous dispersal and *Mericarpaea* distinguished by the hooked bristles on the fruits. Both genera are centered in southwestern Asia and suggest an unexpected, morphologically dramatic phylogenetic divergence within clade VA. Soza and Olmstead (2010a) came to similar results with *Callipeltis* but had no material of *Mericarpaea*. No DNA analyses are available yet from some southwestern to central Asiatic taxa of the traditional genus *Asperula*, that is, the perennials of *Asperula* sect. *Oppositifolia* Shishk ex Schönb.-Tem. (ca. 20 species) and four annual species that include the former genus *Leptunis* (Ehrendorfer et al., 2005). It is likely that they, too, group with clade VA.

Another unexpected relationship of clades, well supported by our DNA data, is encountered in group VB (Figs. 1, 2), where the traditional *Asperula* s. str. and *Galium* sect. *Jubogalium* (the latter not studied before) form highly supported sisters (100% bootstrap). *Asperula* s. str., a small group with about four species, is characterized by involucrate capitula of funnel-shaped flowers and includes perennial (*A. taurina* L.) and annual (*A. arvensis* L., etc.) taxa centered in the southeastern Mediterranean and southwestern Asiatic region. The more speciose *Galium* sect. *Jubogalium* (ca. 13 species) with rotate flowers and a particular truncate ovary structure and indumentum includes more xerophytic perennial and annual taxa, which extend from southeastern Arabia and Southwest Asia throughout the entire Mediterranean region (Ehrendorfer, 1958).

Even more heterogeneous and mostly perennial is group VC (Figs. 1, 2), partly recognized already by Manen et al. (1994) as their *Asperula* sect. *Glabella* clade and verified by Soza and Olmstead (2010a) as clade V. At its base we find *Galium* sect. *Depauperata* s. str., an aberrant group of three annual species with whorls of two leaves and two smaller leaflike stipules and fruits with uncinate bristles, ranging from central Asia to western North America. The core of clade VC consists of the mesophilous and strongly disjunct *Asperula* sect. *Glabella*, traditionally composed of ca. 13 species and extending from the Mediterranean (e.g., *A. laevigata* L.) to eastern Asia (i.e., *A. maximoviczii* Kom. $\equiv$ *G. maximoviczii* (Kom.) Pobed. on the Asiatic mainland and *A. trifida* Makino in Japan). *Asperula* sect. *Glabella* is closely linked to the also perennial but hygrophilous *Galium* sect. *Aparinoides*, quite speciose with ca. 20 worldwide distributed species (Puff, 1974). This group occurs throughout the Northern Hemisphere from North America (e.g., *G. obtusum* Bigelow) to Eurasia (e.g., *G. palustre* L.) and reaches the Arctic (*G. trifidum* L.), Africa, and southern South America (e.g., *G. antarcticum* Hook. f.). It is remarkable that the analyzed plastid DNA of *Galium* sect. *Aparinoides* has been found to be nearly identical with that of the morphologically quite distinct dioecious *Asperula* sect. *Dioicae* in Australia and New Zealand (22 species). Recent and still unpublished studies (2014) have supported these close affinities.

Clade VD (Figs. 1, 2) has been recognized already by Manen et al. (1994) and was designated herein as the *Cruciata* clade. This species group includes a large portion of the traditional genus *Galium*, in particular *Galium* sect. *Platygalium* s.l. and its

numerous relatives (as verified and greatly extended by Soza & Olmstead, 2010a, 2010b), possibly with > 250 species. Generally, members of clade VD are characterized by whorls of two leaves and only two similar leaflike stipular derivatives, all not rarely with three (or even more) parallel main veins. Its more plesiomorphic core (*Galium* sect. *Platygalium* s. str.) consists of perennial taxa with closed thyrsoid inflorescences (terminating in a flower), rotate 4-lobed hermaphroditic flowers without an involucrum of bracteoles, and dry mericarps often with hooked bristles or various hairs. Corresponding taxa have a worldwide distribution, from Eurasia to Africa, Australia, and New Zealand (Thompson, 2009) and the Americas. No DNA sequences are yet available for the monotypic genus *Microphysa* with *M. elongata* (Schrenk) Pobed. (≡ *Asperula elongata* Schrenk) endemic to central Asia, but from its morphology and similarity to *G. rubioides* L. it is very likely that it represents only an aberrant taxon within *Galium* sect. *Platygalium* (Chen & Ehrendorfer, 2011). The data presented by Soza and Olmstead (2010b) demonstrate that nearly all New World clades of group VD have originated by evolutionary budding (Hörandl & Stuessy, 2010) and divergent evolutionary radiation from a little-changed ancestor similar to *G. oreganum* Britton. This extant species from northwestern California to western Oregon and Washington is a plesiomorphic member of *Galium* sect. *Platygalium*. In contrast, the derived and mostly more apomorphic clades 1 to 9, as proposed by Soza and Olmstead (2010b: fig. 2), vary from perennial to annual, from hermaphroditic to polygamous and dioecious, from pedicillate and bare to sessile flowers with bracteolate involucra (*Relbunium*, sensu Ehrendorfer, 1955; Dempster 1982, 1990), and from dry mericarps with hooked to straight hairs (*Galium* sect. *Lophogalium*) to glabrous and repeatedly even to fleshy fruits (*Bataprine*, Californian taxa: Dempster & Stebbins, 1968; *Relbunium*, Central to South American taxa: Ehrendorfer, 1955). In many cases morphologically circumscribed New World groups are difficult to reconcile with the clades suggested by the DNA data (Soza & Olmstead, 2010a, 2010b). Creating supraspecific taxa without the near-ancestral *G. oreganum* would again result in problems with paraphyly.

In contrast to *Galium* sect. *Platygalium* s.l. with closed inflorescences and terminal flowers, the clade VD (Figs. 1, 2) also includes the early recognized and clearly related smaller genera *Cruciata* (ca. 12 species, western Eurasia) and *Valantia* (ca. seven species across the Mediterranean region). They are characterized by apomorphic, open inflorescences that have only lateral floriferous cymes and vegetative apical growth. Both genera include perennials and annuals, and both exhibit increasing specializations with respect to fruit dispersal (Ehrendorfer, 1965).

The last and also quite speciose element of the superclade SC is clade VI (Figs. 1, 2). It corresponds to the *Galium* sect. *Galium* clade of Manen et al. (1994), has been fully supported most recently by Soza and Olmstead (2010a, their clade III), and corresponds to our *Galium* s. str. (Figs. 1, 2). It includes the type species of the genus (*G. verum* L.) in *Galium* sect. *Galium* and species from about eight other sections, encompassing > 200 species. Morphologically, *Galium* s. str. is characterized by whorls of leaves and leaflike stipular derivatives with more than four (≤ 12) elements on well-developed stems, by the single main vein to the leaf, the terminal and closed thyrsoid inflorescences, rotate (only rarely funnel-shaped), 4-lobed hermaphrodite flowers, and dry mericarps, sometimes with hooked bristles, various hairs or often glabrous.

The natural distribution of *Galium* s. str. is concentrated in the Old World, with centers of diversity in eastern and southwestern Asia but also in Africa. Apart from introduced taxa, only a few species have reached North America (e.g., *G. asprellum* Michx., *G. concinnum* Torr. & A. Gray, *G. mexicanum* Kunth, and *G. triflorum* Michx. from *Galium* sect. *Trachygalium*, and possibly *G. aparine* L. s.l. from *Galium* sect. *Aparine*), but none in South America (*G. surinamense* Dempster is highly doubtful).

The internal relationships of *Galium* s. str. (clade VI, see Fig. 2) are complex. With eastern Asian members of *Galium* sect. *Hylaea*, particularly *G. hoffmeisteri* (Klotzsch) Ehrend. & Schönb.-Tem. ex R. R. Mill, clade VI is morphologically clearly linked to *G. paradoxum* (only species of clade IV, *Galium* sect. *Cymogalia*) by remarkable morphological similarities in life form, inflorescence, and hooked bristles on its dry mericarps. This linkage at the very base of the SC superclade and *Galium* s.l. (Figs. 1, 2), together with the available DNA data, suggest that *Galium* sect. *Hylaea*, limited with about eight species to Eurasia, is relatively plesiomorphic and occupies a basal and paraphyletic position within clade VI (see Fig. 2) because all other sections of this clade presumably have originated from similar ancestors. *Galium* sect. *Trachygalium* is closely linked to *Galium* sect. *Hylaea* by *G. triflorum*, which combines its creeping rhizomes, leaf morphology, and hooked fruit bristles with partly retrorsely aculeolate stems. The latter characterizes *Galium* sect. *Trachygalium*, a diverse and still poorly understood section with ca. 50 species, which has aberrant members in Africa (e.g., *G. tomentosum* Thunb.) and Madagascar (e.g., *G.*

polyacanthum (Baker) Puff) and extends from Eurasia to North America. In Asia and Africa, *Galium* sect. *Trachygalium* is not clearly separable from the speciose *Galium* sect. *Galium*, including *Galium* sect. *Leiogalium* (≤ 100 or more species), which is centered in western Eurasia and the Mediterranean region. *Galium* sect. *Orientigalium* has its greatest diversity in southwestern Asia (> 50 species) and connects *Galium* sect. *Galium* with *Galium* sect. *Leptogalium* (ca. 42 species) in the western Mediterranean and Europe. For all these perennial sections, one should consult Ehrendorfer et al. (1976, 2005) and Chen and Ehrendorfer (2011). It is obvious that their taxonomic limits are somewhat vague, and none are clearly defined by available DNA sequences or by morphological criteria. Nevertheless, the data of Soza and Olmstead (2010a) and Ehrendorfer et al. (2011, and in prep.) give clear evidence on the independent and parallel origins of annual taxa from perennial sections of *Galium* s. str., particularly in the Mediterranean region and Southwest Asia. This refers to the annual sections *Galium* sect. *Aparine* (about eight species) and *Galium* sect. *Kolgyda* s. str. (three species), apparently derived from ancestors among the perennial *Galium* sect. *Hylaea*, as well as to the annual section *Galium* sect. *Microgalium* (ca. 15 species), closely related to perennials of *Galium* sect. *Leptogalium*.

General Conclusions

From our present understanding of the phylogenetic relationships of the Rubieae clades, it is obvious that today's taxonomic subdivisions within the tribe are still strongly influenced by tradition and should not be maintained. If taxonomy is expected to reflect evolutionary differentiation and affinities by descent, we need to revise the supraspecific taxonomy of Rubieae.

The first and obviously necessary step in this direction is the elimination of clearly polyphyletic taxa as *Asperula* s.l. Nevertheless, problems arise with paraphyly and from the cladistic postulate that only holophyletic taxa are acceptable, which include common ancestors as well as all of their descendants. If this postulate is violated, we will be accused of creating unacceptable paraphyletic taxa. Or should we interpret all extant ancestor-like plesiomorphic relics and descendant-like apomorphic expansive newcomers simply as phylogenetic sisters? Is this a legitimate way to eliminate many critical cases of paraphyly, or should we rather accept such paraphyletic supraspecific taxa? Thus, contrary to the arguments recently summarized by Schmidt-Lebuhn (2011) and in agreement with Hörandl (2006, 2007), Stuessy (2009), Hörandl and Stuessy (2010), and many others, we prefer the latter, less rigid, evolutionary, and also morphologically plausible approach: we accept paraphyly in DNA-supported cases, where extant, relatively plesiomorphic and rather unchanged ancestor-like taxa in their geological past appear to have given rise to strongly deviating and clearly more apomorphic descendant taxa (see Schmidt-Lebhuhn, 2011: fig. 2). Relevant examples from Rubieae discussed herein are that *Kelloggia* lies basal to all remaining Rubieae, followed by the well-supported distinction of *Didymaea* and *Rubia* from a remaining superclade of *Galium* s.l.; that *Galium* sect. *Cymogalia* is strongly supported as basal to the remaining species groups of *Galium* s.l.; that *Asperula* sect. *Cruciana* is suggested to be affined with *Crucianella*, *Phuopsis*, *Sherardia*, and the *Asperula* sections *Cynanchicae*, *Hexaphylla*, and *Thliphthisa*; that *Asperula* sect. *Glabella* is strongly supported as basal to *Galium* sect. *Aparinoides* and *Asperula* sect. *Dioicae*; that *Galium* sect. *Platygalium* appears to be derivative to *Relbunium*, *Bataprine*, and to many other species groups in the New World; that, furthermore, *Galium* sect. *Platygalium* is well supported in its affiliation with both *Cruciata* and *Valantia*; and that the perennial *Galium* sect. *Hylaea* can be postulated as basal to the annual *Galium* sect. *Aparine* and *Galium* sect. *Kolgyda* s. str., whereas *Galium* sect. *Leptogalium* apparently is derivative to the annual *Galium* sect. *Microgalium*.

Should one give preference to splitting or to lumping to improve the traditional Rubieae taxonomy? This question is not easy to answer, particularly with respect to the superclade of *Galium* s.l. (Fig. 2). In the case of splitting one could maintain the well-established and unproblematic genera *Asperula* s. str., *Callipeltis*, *Crucianella*, *Cruciata*, *Galium* s. str., *Mericarpaea*, *Phuopsis*, *Sherardia*, and *Valantia*. For the current *Asperula* sections—*Asperula* sect. *Cruciana*, *Asperula* sect. *Cynanchicae*, *Asperula* sect. *Glabella*, *Asperula* sect. *Hexaphylla*, and *Asperula* sect. *Thliphthisa*—and for the *Galium* sections—*Galium* sect. *Aparinoides*, *Galium* sect. *Cymogalia*, *Galium* sect. *Depauperata*, and *Galium* sect. *Platygalium*—one would have to create seven to nine new genera. If lumping is preferred, all of the aforementioned genera and sections evidently would have to be united and partly renamed under *Galium* s.l., together with the creation of a new and rather complex infrageneric taxonomical hierarchy to reflect affinities between the many subunits. Both approaches would be compatible with our present knowledge of phylogeny within Rubieae. Nevertheless, for practical reasons we strongly favor the splitting

alternative because it makes relationships within the speciose Rubieae better visible on the binomial level and can be achieved with fewer nomenclatural changes. We hope to approach this goal by a thoroughly documented and species-based phylogenetic analysis, which is in preparation.

Literature Cited

Boissier, E. 1875. Flora Orientalis 3: 12–84. H. Georg, Lyon.

Bremer. B. & J.-F. Manen. 2000. Phylogeny and classification of the subfamily Rubioideae (Rubiaceae). Pl. Syst. Evol. 225: 43–72.

Bremer, B. & T. Eriksson. 2009. Time tree of Rubiaceae: Phylogeny and dating the family, subfamilies, and tribes. Int. J. Pl. Sci. 170: 766–793.

Candolle, A. P. de. 1830. Prodromus Systematis Naturalis Regni Vegetabilis 4: 580–614. Treuttel & Würz, Paris.

Chen, T. & F. Ehrendorfer. 2011. Rubiaceae–Rubieae: *Asperula*, *Galium*, *Kelloggia*, *Leptunis*, *Microphysa*, *Phuopsis*, *Rubia*. Pp. 77–78, 104–141, 183–184, 212–213, 216–217, 291, 305–319 *in* W. Zhengyi, P. H. Raven & H. Deyuan (editors), Flora of China, Vol. 19 (Cucurbitaceae through Valerianaceae with Annonaceae and Berberidaceae). Science Press, Beijing, and Missouri Botanical Garden Press, St. Louis.

Dempster, L. T. 1980. The genus *Galium* section *Lophogalium* (Rubiaceae) in South America. Allertonia 2: 247–279.

Dempster, L. T. 1982. The genus *Galium* (Rubiaceae) in South America III. Allertonia 3: 211–258.

Dempster, L. T. 1990. The genus *Galium* (Rubiaceae) in South America. IV. Allertonia 5: 283–345.

Dempster, L. T. & G. L. Stebbins. 1968. A cytotaxonomic revision of the fleshy-fruited *Galium* species of California and southern Oregon. Univ. Calif. Publ. Bot. 46: 1–52.

Ehrendorfer, F. 1955. Revision of the genus *Relbunium* (Endl.) Benth. & Hook. (Rubiaceae-Galieae). Bot. Jahrb. Syst. 76: 516–553.

Ehrendorfer, F. 1958. Sect. nova *Jubo-Galium* (Rubiaceae: *Galium*), ein alter aufgesplitterter Sippenkomplex mit Zentrum im südöstlichen Mittelmeergebiet. Zur Phylogenie der Gattung *Galium*, V. Pl. Syst. Evol. 105: 212–228.

Ehrendorfer, F. 1965. Dispersal mechanisms, genetic systems, and colonizing abilities in some flowering plant families. Pp. 331–351 *in* H. G. Baker & G. L. Stebbins (editors), Genetics of Colonizing Species. Academic Press, New York.

Ehrendorfer, F. 1975. Intrageneric taxa in European Rubiaceae: *Asperula* and *Galium*. Bot. J. Linn. Soc. 70: 2–6.

Ehrendorfer, F., F. Krendl & C. Puff. 1976. *Sherardia*, *Crucianella*, *Asperula*, *Galium*, *Callipeltis*, *Cruciata*, *Valantia*, *Rubia*. Pp. 3–38 *in* T. G. Tutin, V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters & D. A. Webb (editors), Flora Europaea, Vol. 4. Cambridge University Press, Cambridge.

Ehrendorfer, F. & E. Schönbeck-Temesy. 1982. Rubiaceae. Pp. 722–861, 895–900 *in* P. H. Davis (editor), Flora of Turkey and the East Aegean Islands, Vol. 7. University Press, Edinburgh.

Ehrendorfer, F., J.-F. Manen & A. Natali. 1994. cpDNA intergene sequences corroborate restriction site data for reconstructing Rubiaceae phylogeny. Pl. Syst. Evol. 190: 195–211.

Ehrendorfer, F., E. Schönbeck-Temesy, C. Puff & W. Rechinger. 2005. Rubiaceae. Part 176 *in* K. H. Rechinger (editor), Flora Iranica. Verlag Naturhistorisches Museum, Vienna.

Ehrendorfer, F., V. Vladimirov & M. Barfuss. 2011. Worldwide radiation, phylogeography and paraphyly in the speciose Rubiaceae-Rubieae. Pp. 253–254 *in* Abstract book, IBC2011, XVIII International Botanical Congress, 23–30 July 2011, Melbourne.

Grisebach, A. 1844. Pp. 155–169 *in* Spicilegium Florae Rumelicae et Bithynicae, Vol. 2. Vieweg, Brunsvigae.

Hörandl, E. 2006. Paraphyletic versus monophyletic taxa—Evolutionary versus cladistic classification. Taxon 55: 564–579.

Hörandl, E. 2007. Neglecting phylogeny is bad taxonomy. Taxon 56: 1–5.

Hörandl, E. & T. F. Stuessy. 2010. Paraphyletic groups as natural units of biological classification. Taxon 59: 1641–1653.

Jelenevsky, A., N. Kuranova & S. Pjatunina. 2003. De sectionibus in genere *Galium* L. (Rubiaceae). Novosti Sist. Vyssh. Rast. 35: 174–187.

Koch, W. D. J. 1843. Synopsis Florae Germanicae et Helveticae, 2nd ed. F. Wilmans, Frankfurt.

Ledebour, C. F. 1844. Flora Rossica 2: 396–422. Schweizerbart, Stuttgart.

Manen, J.-F. 2000. Relaxation of constraints in promoters of the plastid gene *atp*B in a particular Rubiaceae lineage. Pl. Syst. Evol. 224: 235–241.

Manen, J.-F. & A. Natali. 1995. Comparison of the evolution of ribulose-1, 5-biphosphate carboxylase (*rbc*L) and *atp*B-*rbc*L non-coding spacer sequences in a recent plant group, the tribe Rubieae (Rubiaceae). J. Molec. Evol. 41: 920–927.

Manen, J.-F. & A. Natali. 1996. The chloroplast *atp*B-*rbc*L spacer in Rubiaceae. Opera Bot. Belg. 7: 51–57.

Manen, J.-F., A. Natali & F. Ehrendorfer. 1994. Phylogeny of the Rubiaceae-Rubieae inferred from the sequence of a cpDNA intergene region. Pl. Syst. Evol. 190: 195–211.

Natali, A. & J.-F. Manen. 1995. The phylogenetic reconstruction inferred from a cpDNA intergene region as a framework for the taxonomic revision of a systematic group: The example of the tribe Rubieae (Rubiaceae). Giorn. Bot. Ital. 129: 57–66.

Natali, A., J.-F. Manen, M. Kiehn & F. Ehrendorfer. 1995. Phylogeny of the Rubiaceae-Rubioideae, in particular the tribe Rubieae: Evidence from a non-coding chloroplast DNA sequence. Ann. Missouri Bot. Gard. 82: 428–439.

Natali, A., J.-F. Manen, M. Kiehn & F. Ehrendorfer. 1996. Tribal, generic, and specific relationships in the Rubioideae-Rubieae (Rubiaceae) based on sequence data of a cpDNA intergene region. Opera Bot. Belg. 7: 193–203.

Nie, Z.-L., J. Wen, H. Sun & B. Bartholomew. 2005. Monophyly of *Kelloggia* Torrey ex Benth. (Rubiaceae) and evolution of its intercontinental disjunction between western North America and eastern Asia. Amer. J. Bot. 92: 642–652.

Puff, Ch. 1974. Biosystematik der Formenkreise um *Galium palustre* L. und *G. trifidum* L.(Rubiaceae) auf der Nord- und Südhemisphäre. Dissertation, Faculty of Philosophy, University of Vienna, Vienna.

Robbrecht, E. 1988. Tropical woody Rubiaceae. Characteristic features and progressions. Contributions to a new subfamilial classification. Opera Bot. Belg. 1: 1–171.

Robbrecht, E. & J.-F. Manen. 2006. The major evolutionary lineages of the coffee family (Rubiaceae, angiosperms). Combined analysis (nrDNA and cpDNA) to infer the position of *Coptosapelta* and *Luculia*, and supertree construction based on *rpcL*, *rps16*, *trnL-trnF* and *atpB-rbcL* data. A new classification in two subfamilies, Cinchonoideae and Rubioideae. Syst. & Geogr. Pl. 76: 85–146.

Schmidt-Lebuhn, A. N. 2011. Fallacies and false premises—A critical assessment of the arguments for the recognition of paraphyletic taxa in botany. Cladistics 27: 1–14.

Schumann, K. 1897. Rubiaceae. Pp. 1–156 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, Vol. 4(4). Wilhelm Engelmann, Leipzig.

Shishkin, B. K., E. G. Linczevski, E. G. Pobedimova, M. W. Klokov & A. I. Pojarkova. 1958. Rubiaceae. Pp. 164–419, 687–726 *in* B. K. Shishkin & E. G. Bobrov (editors), Flora of the U.S.S.R., Vol. 23. Akademiya nauk, Leningrad.

Soza, V. L. & R. G. Olmstead. 2010a. Molecular systematics of tribe Rubieae (Rubiaceae): Evolution of major clades, development of leaf-like whorls, and biogeography. Taxon 53: 755–771.

Soza, V. L. & R. G. Olmstead. 2010b. Evolution of breeding systems and fruits in New World *Galium* and relatives (Rubiaceae). Amer. J. Bot. 97: 1630–1646.

Stuessy, T. 2009. Plant Taxonomy: The Systematic Evaluation of Comparative Data, 2nd ed. Columbia University Press, New York.

Thompson, J. R. 2009. Revision of *Asperula* and *Galium* (Rubieae: Rubiaceae) in Australia. Muelleria 27: 36–112.

APPENDIX 1. List of taxonomic names of genera (in boldface) and sections within Rubieae (Rubiaceae) examined in the present study. *Bataprine* Nieuwl., *Microphysa* Schrenk, *Leptunis* Stev. (missing in the present molecular analysis), and *Relbunium* (Endl.) Benth. & Hook. f. are not accepted herein as genera. Apparently they have to be included in *Galium* sect. *Platygalium* s.l., with only *Leptunis* Stev. in *Asperula* sect. *Trichodes* Boiss., near section *Cruciana* Griseb.

Asperula L., Sp. Pl. 1: 103. 1753. *Asperula* L. sect. *Asperula*. TYPE: *Asperula arvensis* L.

Asperula L. sect. *Cruciana* Griseb., Spic. Fl. Rumel. 2: 166. 1846. TYPE: *Asperula glomerata* (M. Bieb.) Griseb.

Asperula L. sect. *Cynanchicae* (DC.) Boiss., Diagn. Pl. Orient, ser. 1, 3: 31. 1843. TYPE: *Asperula cynanchica* L.

Asperula L. sect. *Dioicae* Airy Shaw & Turrill, Bull. Misc. Inform. Kew 1928 (3): 82. 1928. LECTOTYPE: *Asperula conferta* Hook. f., designated by Ehrendorfer here.

Asperula L. sect. *Glabella* Griseb., Spic. Fl. Rumel. 2: 166. 1846. LECTOTYPE: *Asperula involucrata* Wahlenb., designated by Ehrendorfer, Bot. J. Linn. Soc. 70: 2, 1975.

Asperula L. sect. *Hexaphylla* Ehrend., Bot. J. Linn. Soc. 70(1): 2. 1975. TYPE: *Asperula hexaphylla* All.

Asperula L. sect. *Oppositifolia* Shishk. ex Schönb.-Tem., Pl. Syst. Evol. 174: 197 (1991). TYPE: *Asperula oppositifolia* Regel & Schmalh.

Asperula sect. *Thliphthisa* (Griseb.) Ehrend., J. Linn. Soc., Bot. 70: 3. 1975. *Galium* sect. *Thliphthisa* Griseb., Spic. Fl. Rumel. 2: 161. 1846. TYPE: *Galium rupestre* Vis. [= *Asperula scutellaris* Vis.].

Bataprine Nieuwl., Amer. Midl. Naturalist 1: 264. 1910. TYPE: *Bataprine hispidula* (Michx.) Nieuwl. ≡ *Galium hispidulum* Michx.

Callipeltis Steven, Observ. Pl. Ross. (2): 69. 1828. [1824–Sep. 1828]); Nouv. Mém. Soc. Imp. Naturalistes Moscou 1: 275. 1829: TYPE: *Callipeltis cucullaris* (L.) DC., as "*cucullaria*" 1830, non *Callipeltis cucullaris* Steven, nom. inval., 1829.

Crucianella L., Sp. Pl. 1: 108. 1753. TYPE: *Crucianella latifolia* L.

Cruciata Mill., Gard. Dict. Abr. (ed. 4). 1754. *Galium* sect. *Cruciata* W. D. J. Koch, Syn. Fl. Germ. Helv. (ed. 2): 361. 1843. TYPE: *Cruciata laevipes* Opiz.

Didymaea Hook. f., Gen. Pl. [Bentham & Hooker f.] 2: 150. 1873. TYPE: *Didymaea mexicana* Hook. f.

Galium L., Sp. Pl. 1: 105. 1753. *Galium* L. sect. *Galium* [≡ *Galium* sect. *Eugalium* (DC.) W. D. J. Koch, Syn. Fl. Germ. Helv. (ed. 2): 364. 1843]. TYPE: *Galium verum* L.

Galium L. sect. *Aparine* W. D. J. Koch, Syn. Fl. Germ. Helv. (ed. 2): 362. 1843. TYPE: *Galium aparine* L.

Galium L. sect. *Aparinoides* (Jord.) Gren. Fl. France [Grenier] 2: 15, 39. 1851. TYPE: *Galium palustre* L.

Galium L. sect. *Cymogalia* Pobed. s. str., Fl. URSS 23: 712. 1958. TYPE: *Galium paradoxum* Maxim.

Galium L. sect. *Depauperata* Pobed., Fl. URSS 23: 709. 1958. LECTOTYPE: *Galium songaricum* Schrenk ex Fisch. & C. A. Mey., designated by Ehrendorfer here.

Galium L. sect. *Hylaea* (Griseb.) Ehrend., Bot. J. Linn. Soc. 70: 3. 1975. *Asperula* sect. *Hylaea* Griseb., Spic. Fl. Rumel. 2: 167. 1844. TYPE: *Galium odoratum* (L.) Scop.

Galium L. sect. *Jubogalium* Ehrend., Oesterr. Bot. Z. 105: 212. 1958. TYPE: *Galium graecum* L.

Galium L. sect. *Kolgyda* Dumort., Fl. Belg. [Dumortier] 55. 1827. TYPE: *Galium tricornutum* Dandy (= *Galium tricorne* Stokes in With., nom. superfl., p.p.), designated by Ehrendorfer, Fl. Iranica 176: 233. 2005.

Galium L. sect. *Leiogalium* (DC.) Ledeb., Fl. Ross. [Ledebour] 2: 406. 1844. TYPE: *Galium sylvaticum* L., designated by Ehrendorfer here.

Galium L. sect. *Leptogalium* Lange in Willk., Prodr. Fl. Hispan. 2: 316. 1870. TYPE: *Galium pumilum* Murray (= *Galium sylvestre* Pollich, nom. illeg., non *Gallium sylvestre* Scop.), designated by Ehrendorfer, Sitzungsber. Österr. Akad. Wiss., Math.-Naturwiss. Kl., Abt. I, 169(9–10): 407. 1960.

Galium L. sect. *Lophogalium* K. Schum., Nat. Pflanzenfam. [Engler & Prantl] 4(4): 152. 1897. TYPE: *Galium multiflorum* Kellogg, designated here.

Galium L. sect. *Microgalium* Griseb., Spic. Fl. Rumel. 2: 161. 1844. TYPE: *Galium tenuissimum* M. Bieb., designated by Ehrendorfer here.

Galium L. sect. *Orientigalium* Ehrend., Oesterr. Bot. Z. 98: 435. 1951. TYPE: *Galium subvelutinum* (DC.) K. Koch.

Galium L. sect. *Platygalium* (DC.) W. D. J. Koch, Syn. Fl. Germ. Helv. (ed. 2): 364. 1843. *Galium* [unranked] *Platygalia* DC., Prodr. [A. P. de Candolle] 4: 598. 1830. *Galium* ser. *Platygalium* (DC.) Ortega Oliv. & Devesa, Acta Bot. Malac. 29: 245. 2004. TYPE: *Galium rubioides* L., designated by Ehrendorfer in Fl. Iranica 176: 175, 2005.

Galium L. sect. *Trachygalium* K. Schum., Nat. Pflanzenfam. [Engler & Prantl] 4 (4): 151. 1897. TYPE: *Galium uliginosum* L., designated by Ehrendorfer in Fl. Iranica 176: 185, 2005.

Kelloggia Torr. in Benth. & Hook. f., Gen. Pl. [Bentham & Hooker f.] 2: 137. 1873. TYPE: *Kelloggia galioides* Torr.

Leptunis Stev., Bull. Soc. Imp. Nat. Mosc. 29: 366. 1856. *Asperula* sect. *Trichodes* Boiss., Fl. Orient. 3: 31. 1875. TYPE: *Leptunis tenuis* Stev. [= *Leptunis trichodes* (J. Gay ex DC.) Shishk. ≡ *Asperula trichodes* J. Gay ex DC.].

Mericarpaea Boiss., Diagn. Pl. Orient., ser. 1, 3: 51. 1843. TYPE: *Mericarpaea vaillantioides* Boiss. [= *Mericarpaea ciliata (*Banks & Sol.) Eig].

Microphysa Schrenk, Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg 2 : 115. 1844. TYPE: *Microphysa elongata* (Schrenk)Pobed. [≡ *Asperula elongata* Schrenk = *Microphysa galioides* Schrenk].

Phuopsis (Griseb.) Benth. & Hook. f., Gen. Pl. [Bentham & Hooker f.] 2: 151. 1873. *Asperula* sect. *Phuopsis* Griseb., Spic. Fl. Rumel. 2: 167. 1846. TYPE: *Crucianella stylosa* Trin. [= *Phuopsis stylosa* (Trin.) Hook. f. ex B. D. Jacks.].

Relbunium (Endl.) Benth. & Hook. f., Gen. Pl. [Bentham & Hooker f.] 2: 149. 1873. ≡ *Galium* sect. *Relbunium* Endl., Gen. Pl. [Enlicher]: 523. 1839. ≡ *Rubia* L. subgen. *Relbunium* (Endl.) Rchb. f., Repert. Bot. Syst. 1: 74. 1842. TYPE: *Valantia hypocarpia* L. [≡ *Galium hypocarpium* (L.) Endl. ex Griseb., ≡ *Relbunium hypocarpium* (L.) Hemsl., designated by Ehrendorfer, Bot. Jahrb. 76: 518. 1955.

Rubia L., Sp. Pl. 1: 109. 1753. TYPE: *Rubia tinctorum* L.

Sherardia L., Sp. Pl. 1: 102. 1753.: *Sherardia arvensis* L.

Valantia L., Sp. Pl. 2: 1051. 1753. TYPE: *Valantia muralis* L., designated by Britton, Fl. Bermuda, 366. 1918.